

TAXONOMIC STATUS OF *THELEGNATHUS BROWNI* BROOM, A PROCOLOPHONID REPTILE FROM THE SOUTH AFRICAN TRIASSIC

SEAN P. MODESTO

Rea Postdoctoral Fellow, Section of Vertebrate Paleontology

ROSS J. DAMIANI¹

ABSTRACT

The holotype of the procolophonid reptile *Thelegnathus browni*, from the Early-to-Middle Triassic *Cynognathus* Assemblage Zone of the Beaufort Group, South Africa, consists of an isolated left maxilla that was originally described by Robert Broom early last century. This specimen is redescribed and compared with maxillae of more recently described procolophonid taxa from Eastern Europe and North America. A single apomorphy, the presence of marginal teeth that increase in mesiodistal diameter posteriorly, was proposed to diagnose the genus *Thelegnathus*. However, this character is present also in several Laurasian procolophonid genera. The specific diagnostic features of *T. browni* are either plesiomorphic for procolophonids or are of doubtful taxonomic value. Accordingly, *T. browni* is declared a nomen dubium, and the four species from the *Cynognathus* Assemblage Zone recently assigned to *Thelegnathus* are transferred to new genera. The following replacement names are proposed for these species: *Theleperpeton* gen. nov., for *T. oppressus*; *Theledectes* gen. nov., for *T. perforatus*; *Thelephon* gen. nov., for *T. contritus*; and *Teratophon* gen. nov., for *T. spinigenis*. These taxonomic revisions suggest that there is no basis for a hypothesis that postulates an endemic radiation of procolophonids in central Gondwana (by species of *Thelegnathus*), and indicate that the genus *Thelegnathus* has no utility in biostratigraphic concepts for the Beaufort Group.

KEY WORDS: Procolophonidae (*Thelegnathus*), Reptilia, Triassic, Beaufort Group, South Africa

INTRODUCTION

In the first half of the last century, Robert Broom described a plethora of new synapsids and reptiles from the Permo-Triassic Beaufort Group of the Karoo Basin, South Africa. Most of his new taxa were created for single skulls, but many were based on isolated elements. Among the latter is the maxilla of a small Triassic reptile discovered by Alfred "Gogga" Brown in *Cynognathus* Assemblage Zone strata near Aliwal North (southern Karoo Basin), and subsequently described by Broom (1905) as the new genus and species *Thelegnathus browni*. However, as with many of Brown's discoveries, the precise locality where the specimen was found remains unknown. Broom (1936) later assigned an isolated maxilla and a dentary to *Thelegnathus* (both specimens are now lost: S. Kaal, personal communication), but more complete specimens would not be attributed to the genus for another four decades (Gow, 1977).

Broom (1936) distinguished *Thelegnathus browni* from other procolophonids by tooth morphology: he noted that the teeth of the holotype became progressively greater in mesiodistal diameter towards the posterior of the tooth row. This character was recognized as diagnostic at the generic level by Gow (1977). The curvature of the occlusal plane of the teeth and the nature of the wear on the teeth

¹Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Private Bag 3, Wits 2050, Johannesburg, South Africa.
Submitted 25 March 2002.

were regarded by Gow (1977) as diagnostic at the specific level. There are problems with these diagnostic characters because the holotypic tooth row is damaged posteriorly, and it is unclear if an additional tooth was present. In addition, a number of European and North American procolophonid taxa, unknown during Broom's (1905, 1936) era but known by the time Gow (1977) published his reappraisal, display tooth morphologies and wear reminiscent of the holotype of *Thelegnathus browni*.

Gow (1977) assigned four new species, also from the *Cynognathus* Assemblage Zone in the southern Karoo Basin, to the genus *Thelegnathus*, thereby more than doubling the number of procolophonid species known from that biozone. Gow's (1977) systematic work implies that there was a small, localized radiation of procolophonids in the Karoo Basin in the Early to Middle Triassic. Ivakhnenko (1983), however, expressed doubt that additional species should be assigned to *Thelegnathus*. Ivakhnenko's view was reiterated, in part, by Novikov (1991), who thought that only one of Gow's (1977) species (*T. contritus*) was correctly assigned to *Thelegnathus*.

The recognition of five species of *Thelegnathus* in the *Cynognathus* Assemblage Zone inevitably led to the recognition of a stratigraphic range for the genus (Kitching, 1995). Accordingly, it is possible that *Thelegnathus* may come to play a role in biostratigraphic considerations of that biozone, as has the genus *Procolophon* for the underlying *Lystrosaurus* Assemblage Zone (Groenewald and Kitching, 1995; Neveling et al., 1999). In order to examine monophyly of the genus *Thelegnathus*, and so to assess its potential stratigraphic utility, we reexamined the holotype of *Thelegnathus browni* and compared it to a broad range of procolophonid taxa.

Institutional abbreviations used in this paper: BP, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg; SAM, South African Museum, Cape Town.

SYSTEMATIC PALEONTOLOGY

Reptilia Laurenti, 1768

Parareptilia Olson, 1947

Procolophonia Seeley, 1888

Procolophonidae Lydekker, 1890

Thelegnathus browni Broom, 1905

Holotype.—SAM PK-5869, an isolated left maxilla (Figure 1) preserved in breccia.

Locality and Horizon.—An unknown locality in the Aliwal North District, Eastern Cape Province, South Africa; *Cynognathus* Assemblage Zone, Beaufort Group, Lower or Middle Triassic.

Diagnosis.—Taxon is a nomen dubium.

Description

The holotype has a quadrangular outline in lateral view (Fig. 1A), but the bone is damaged posteriorly and it seems likely, judging from the morphology seen in *Procolophon* (Carroll and Lindsay, 1985) and *Tichvinskia* (Ivakhnenko, 1973), that an anteroposteriorly short edentulous portion has been lost. The maxilla is thickest ventrally and the lateral surface appears to slope gradually towards the dorsal tip.

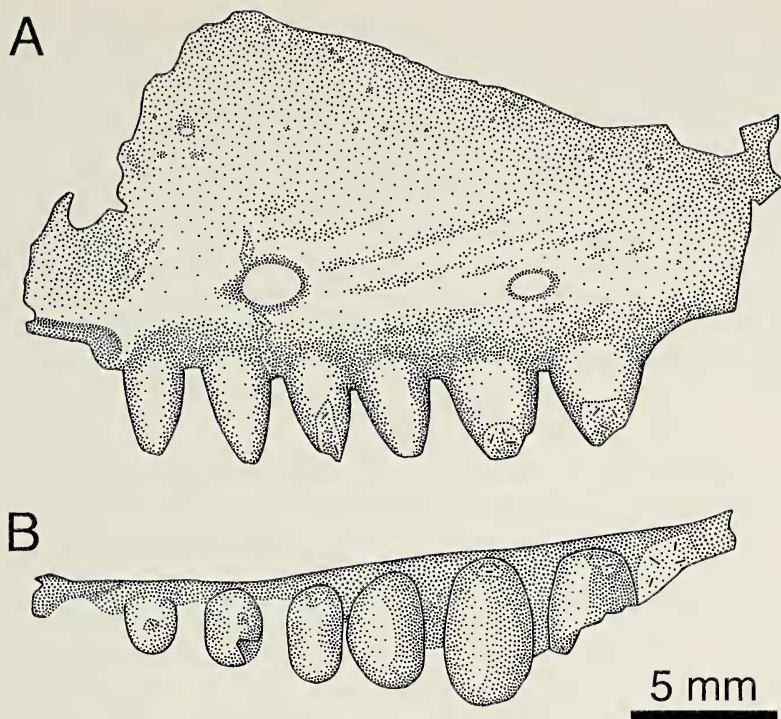


Fig. 1.—*Thelegnathus browni* Broom, holotype SAM PK-5869, left maxilla. A. Lateral view. B. Occlusal view.

The lateral surface is pierced by two large openings, by a smaller opening, and by many fine pits. The largest opening lies just dorsal to the second and third teeth. Judging from its topographical relationships to the ventral margin and the sutural surface for the premaxilla, this opening is the anterolateral foramen (Laurin and Reisz, 1995). It gives rise to a shallow, rapidly attenuating channel that extends anteriorly from the opening. The smaller, posterior opening appears to be a supralabial foramen. It lies in the same approximate position of single or paired foramina that have been illustrated for *Procolophon* (Carroll and Lindsay, 1985) and other procolophonoids (e.g., Modesto et al., 2001). The smallest opening lies dorsal and slightly anterior to the anterolateral foramen, and appears to be a minor nutrient foramen. Tiny pits are positioned diffusely across the dorsal part of the lateral surface.

A series of long, shallow grooves ornament the ventral half of the lateral surface (Fig. 1A). The grooves nearest the ventral margin are anteroposteriorly short and dorsoventrally narrow, but they become longer and broader dorsally and eventually become confluent with the lateral surface. At approximately the same height but at the anterior end of the bone there is a shallow, circular fossa on the lateral surface of the maxilla. This fossa, because it lies directly dorsal to the sutural surface for the premaxilla, appears to be a very shallow version of the maxillary depression seen in *Procolophon*, *Tichvinskia*, and *Contritosauros* (Ivakhnenko, 1973, 1974; Carroll and Lindsay, 1985). None of the skulls described by Gow (1977) feature a maxillary depression.

Six teeth are present. Broom (1936) mentioned the possibility of a seventh tooth, but the ventral surface of the maxilla immediately posterior to the sixth tooth is too damaged to make this determination (Fig. 1B). If a seventh tooth was indeed present, it must have been a small tooth, because the ventral margin of the maxilla slopes upwards immediately posterior to the last preserved tooth (Fig. 1A), and there does not appear to be room for a tooth the size of the posterior two or three teeth. As described by Gow (1977), the teeth increase in both mesiodistal and labiolingual diameter from anterior to posterior. The first tooth is subconical, whereas the succeeding teeth have labial and lingual cusps that resemble those illustrated for *Tichvinskia* and *Macrophon* (Ivakhnenko, 1975: fig. 1). Wear is present on each of the last three teeth as a transverse, crescentic facet running from cusp to cusp on the posterior half of the tooth apex.

Discussion

Thelegnathus browni was distinguished from other procolophonids by Broom (1936) by maxillary teeth that become larger from anterior to posterior in the series. Gow (1977) regarded this characteristic as diagnostic at the generic level. However, it works as a diagnostic character only if comparisons are restricted to the South African procolophonoid genera *Owenetta* and *Procolophon*. If the holotype of *T. browni* is missing a seventh tooth that is smaller than the preceding tooth, then again the diagnosis does not work because *Myocephalus crassidens* (Broom, 1936), also from the *Cynognathus* Assemblage Zone of South Africa, has, except for the posteriormost tooth that is the smallest of the upper dentition, maxillary teeth that increase in size from anterior to posterior. It seems unlikely that *Myocephalus* is a junior synonym of *Thelegnathus*, because the maxillary morphology of the former genus (Modesto, personal observation) is strongly reminiscent of the maxillary morphology of leptopleuronine procolophonids (e.g., Sues et al., 2000), whereas that of *T. browni* is not (Fig. 1).

There are also a number of Laurasian procolophonoid taxa whose teeth can be described as growing larger from the front to the back of the marginal dentition. The molariform teeth of *Kapes amaenus* (Ivakhnenko, 1975), *Samaria concinna* (Novikov, 1991), *Acadiella psalidodon*, *Haligonia bolodon*, and *Scoloparia glyphanondon* (Sues and Baird, 1998) all exhibit a progressive increase in size to the posterior end of the tooth row. It is becoming clear that the phenomenon of marginal teeth that become larger from anterior to posterior in a tooth series is typical of many procolophonid taxa. It may be that this character diagnoses a clade of procolophonids that includes not only *T. browni* and the species described and assigned by Gow (1977) to the genus *Thelegnathus*, but also one that includes other procolophonids that have been described in recent years from both Europe and North America. The most appropriate test of this idea would be a phylogenetic analysis of a variety of procolophonoid taxa in order to see if some or all of the taxa that are characterized by this particular dental phenomenon form a natural group. However, it is ironic that many, if not most, of the taxa that do feature such a dentition are known from very fragmentary remains (partial jaws), and it therefore seems unlikely that parsimony analysis would result in the discovery of only a few (or less) minimum-length trees.

The fragmentary nature of the holotype of *Thelegnathus browni* itself leaves little clues about the affinities of the taxon within Procolophonidae and of the putative monophyly of the genus *Thelegnathus*. Apart from the nature of the

dentition discussed above, the morphology of the holotype is unlike that of the maxillae of the other four species (Gow, 1977) in the presence of a maxillary depression and of ornamentation comprising shallow grooves. The former feature is plesiomorphic for procolophonids because it is seen in *Procolophon trigoniceps* (Carroll and Lindsay, 1985) as well as the more basal procolophonoid *Coletta seca* (Modesto et al., 2002). Therefore, the absence of this fossa in the four species described by Gow (1977) is suggestive of two possibilities: (1) that *T. browni* is the basalmost member of a clade that includes the other four species of *Thelegnathus*, or (2) that these other four species are more closely related to other procolophonids that are also characterized by the loss of the maxillary depression, such as *Hypsognathus* (Sues et al., 2000), than they are to *T. browni*. The “curve of the occlusal plane” and “nature of tooth wear” were thought to be diagnostic for *T. browni* (Gow, 1977), but the former is seen also in *Procolophon* (Carroll and Lindsay, 1985: fig. 5) and *Hypsognathus* (Sues et al., 2000: fig. 2f), and thus is probably symplesiomorphic for procolophonids. The diagnostic utility of tooth wear is debatable given that similar wear is seen in *Tichvinskia* and *Macrophon* (Ivakhnenko, 1975). The presence of shallow grooves on the lateral surface of the maxilla may be an autapomorphy of *T. browni*, as they have not been described in other taxa to our knowledge. However, taking into consideration the small size of many procolophonid specimens and the grinding methods that have been used to prepare some materials, particularly those from South Africa, it is unclear if this kind of ornamentation is more widespread and was unintentionally removed from known materials. It is uncertain even if the presence of such shallow grooves on the external surface of a dermal roofing element is a useful phylogenetic character.

The paucity of phylogenetic information that is offered by SAM PK-5869, the holotype of *Thelegnathus browni*, allows little choice but to regard *T. browni* as a nomen dubium. With *T. browni* a nomen dubium, assignment of additional species to the genus becomes unwarranted. Accordingly, the four species that were assigned to *Thelegnathus* by Gow (1977) require a new generic name. However, because there is no evidence that any of Gow's species are congeneric, we assign a new genus to each species. The authors intend to conduct anatomical reappraisals of all four species in the near future in order to place these species in the context of procolophonoid phylogeny. The systematic paleontology of the four species is as follows:

SYSTEMATIC PALEONTOLOGY

Procolophonidae Lydekker, 1890

Thelerpeton oppressus (Gow) gen. nov.

Etymology.—The replacement genus name is from the Greek words *thele* and *herpeton*, which mean “nipple” and “creeper” (or “crawler”), respectively, and is inspired by Broom's (1905) nomen *Thelegnathus*, which means “nipple jaw”.

Holotype.—BP/1/4538 (formerly “BPI 155”), a skull with poor surface detail (Figure 2).

Locality and Horizon.—The farm Hugoskop in Rouxville District, Free State Province. Subzone B of the *Cynognathus* Assemblage Zone, Beaufort Group, Middle Triassic. The localities from which all of Gow's (1977) specimens were recovered also yielded specimens of the dicynodont genus *Kannemeyeria* (Kitching, 1977), now recognized as an index taxon for the middle part (Subzone B)

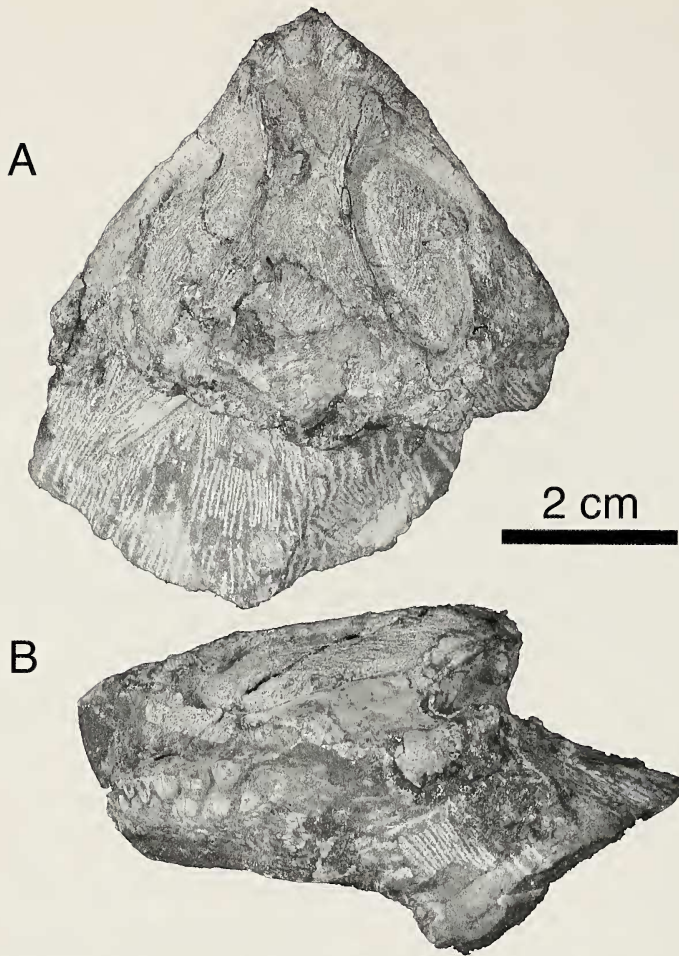


Fig. 2.—*Thelerpeton oppressus* (Gow) gen. nov., holotype BP/1/4538. A. Dorsal view of skull. B. Left lateral view of skull and mandible.

of the *Cynognathus* Assemblage Zone, which is Anisian in age (Hancox et al., 1995).

Diagnosis.—A procolophonid reptile with bulbous marginal teeth “with the crowns pinched up to present a small occlusal area (Gow, 1977, p. 112)”, and dentary dentition that is undercut labially by a continuous, longitudinal sulcus.

Comments.—Bulbous teeth with narrow (“pinched”) apices are present also in the Eastern European genera *Kapes* (Ivakhnenko, 1975) and *Samaria* (= *Orenburgia*: Novikov, 1991), which may be suggestive of close relationships among these taxa. The labial sulcus that undercuts the dentary teeth of *Thelerpeton* is reminiscent of the sulci described for *Contritosaurus* (Ivakhnenko, 1974), but the condition in the latter does not seem to be as developed as that seen in the former taxon. The great posterior expansion of the orbits (past the posteriormost point of the pineal opening) in the holotype suggests that *Thelerpeton oppressus* is a leptopleuronine procolophonid. The dentition of the paratypes, BP/1/4584 and BP/1/4586, differs from that of the holotype in lacking the labial sulcus and being

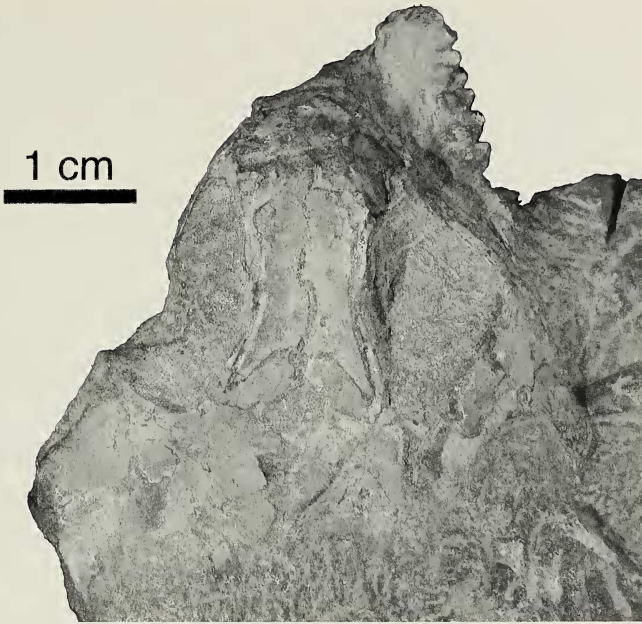


Fig. 3.—*Theledectes perforatus* (Gow) gen. nov., holotype BP/1/4585, skull and right mandibular ramus in dorsal view.

deeply inset from the labial surface. They share the latter feature with the second species described by Gow (1977), *T. perforatus*, the holotype and only known specimen of that species, which is known from the same locality (Hugoskop) as *T. oppressus*. However, there are differences in the dentition, particularly the absence of the autapomorphy of *T. perforatus* (see below), which suggest that BP/1/4584 and BP/1/4586 do not belong to that species.

Theledectes perforatus (Gow) gen. nov.

Etymology.—The replacement genus is derived from the Greek words *thele* and *dektes*, the latter meaning “biter”, which is an oblique reference to the multiple rows of teeth that characterize the taxon. The prefix is inspired by *Thelegnathus* Broom (1905).

Holotype.—BP/1/4585, a dorsoventrally compressed, partial skull (Figure 3).

Locality and Horizon.—The farm Hugoskop in Rouxville District, Free State Province. Subzone B of the *Cynognathus* Assemblage Zone, Beaufort Group, Middle Triassic (Anisian).

Diagnosis.—A procolophonid reptile distinguished from all other parareptiles by the presence of multiple rows of marginal teeth.

Comments.—This species is the sole parareptile with multiple rows of marginal teeth. The only other early reptiles known to have multiple rows of teeth are rhynchosaurs (e.g., Dilkes, 1998) and some captorhinids (e.g., Dodick and Modesto, 1995; Modesto, 1998). The presence of only two incisiform dentary teeth suggests that *Theledectes perforatus* is a basal leptopleuronine, as the same number is found in *Scoloparia glyphanodon* (Sues and Baird, 1998). Four and three incisiform dentary teeth are present in *Tichvinskia vjatkensis* (Ivakhnenko, 1973) and *Procolophon trigoniceps* (Carroll and Lindsay, 1985), respectively; these two

taxa were identified as basal procolophonids in the phylogenetic analysis of Modesto et al. (2002). The distinctive curvature of the labial excavation associated with the deep inseting of the marginal dentition (Gow, 1977; fig. 4C) is reminiscent of the condition seen *Hypsognathus fenneri* (Sues et al., 2000), an observation suggesting that *Theledectes perforatus* is related more closely than *Thelerpeton oppressus* is to leptopleuronine taxa such as *Hypsognathus fenneri*. The presence of single rows of marginal teeth in the *Thelerpeton* paratypes BP/1/4584 and BP/1/4586 implies that these specimens are not assignable to *Theledectes perforatus*.

Thelephon contritus (Gow) gen. nov.

Etymology.—The generic name is from the Greek word *thele* and *-phon*, the latter being the final syllable of *Procolophon*, and now a common suffix in procolophonid generic names (e.g., *Macrophon*, *Microphon*, *Timanophon*).

Holotype.—BP/1/3512, a partial skull lacking the snout and anterior third of the mandible (Figure 4).

Locality and Horizon.—The farm Winnaarsbaken, Burgersdorp District, Eastern Cape Province. Subzone B of the *Cynognathus* Assemblage Zone, Beaufort Group, Middle Triassic (Anisian).

Diagnosis.—This procolophonid is distinguished from other South African species by the presence of a posterior marginal tooth that is almost twice as expanded mediolaterally as the neighboring teeth.

Comments.—This species has no obvious cranial autapomorphies, and its dentition, which was used to distinguish it from the other species assigned to *Thelegnathus* by Gow (1977), resembles in general that of the Laurasian procolophonids *Acadiella psalididon* and *Halogonia bolodon* (Sues and Baird, 1998). The holotype and only known specimen of *Thelephon contritus* does include postcranial material in addition to the skull (Gow, 1977), and it will need to be carefully prepared and redescribed in order to determine if it is a valid species.

Teratophon spinigenis (Gow) gen. nov.

Etymology.—The generic name is from the Greek word *teratos* and *-phon*; the former word means “a wonder” or “monster”, whereas the latter is from *Procolophon*.

Holotype.—BP/1/4299, the nearly complete skull of a large individual (Figure 5).

Locality and Horizon.—The farm Lemoenfontein, Rouxville District, Free State Province. Subzone B of the *Cynognathus* Assemblage Zone, Beaufort Group, Middle Triassic (Anisian).

Diagnosis.—A taxon distinguished from other procolophonids by the presence of a large, posterolaterally-directed spine-like process of the quadratojugal.

Comments.—The quadratojugal process of *Teratophon spinigenis* is like that of *Procolophon trigoniceps* in being a single projection (some leptopleuronines have smaller, multiple spines produced by the quadratojugal), which suggests that *Teratophon* and *Procolophon* are close relatives (Modesto et al., 2002). However, the spine of the former genus is remarkably much larger than that of the latter. Interestingly, the small cheek spine of *Theledectes* resembles that of *Teratophon* in its general morphology, more so than the cheek spine of *Procolophon* (Damiani, personal observation). It is possible that the presence of a single quadratojugal spine, which is considered diagnostic of procolophonines by Modesto et al.

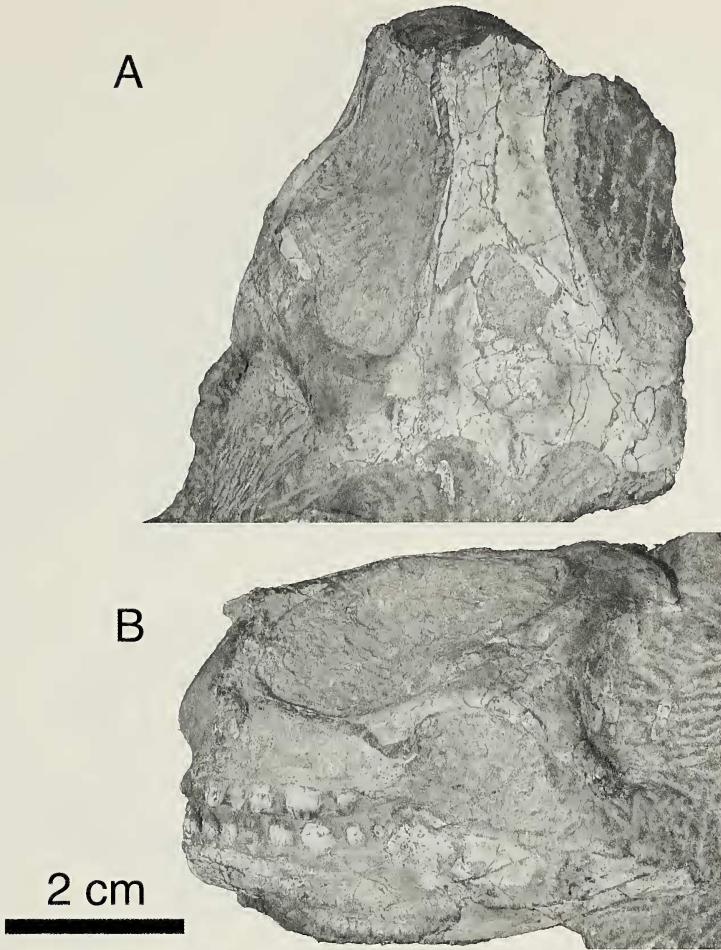


Fig. 4.—*Thelephon contritus* (Gow) gen. nov., holotype BP/1/3512. A. Dorsal view of skull. B. Left lateral view of skull and mandible.

(2002), is instead plesiomorphic with respect to the presence of multiple cheek spines of leptopleuronines.

CONCLUSIONS

The procolophonid *Thelegnathus browni* Broom, known only from a single specimen from the *Cynognathus* Assemblage Zone of the Aliwal North District, South Africa, is a nomen dubium. The sole apomorphy that has been attributed to the genus, the presence of marginal teeth that progressively increase in size towards the posterior end of the tooth row, is shared with a number of Laurasian procolophonids and can no longer be regarded a tenable generic synapomorphy. The four species assigned to the genus by Gow (1977) are, therefore, each assigned a new generic name.

The nomen dubium status of *Thelegnathus browni*, and resultant transfer of *T. oppressus*, *T. perforatus*, *T. contritus*, and *T. spinigenis* to new respective genera,

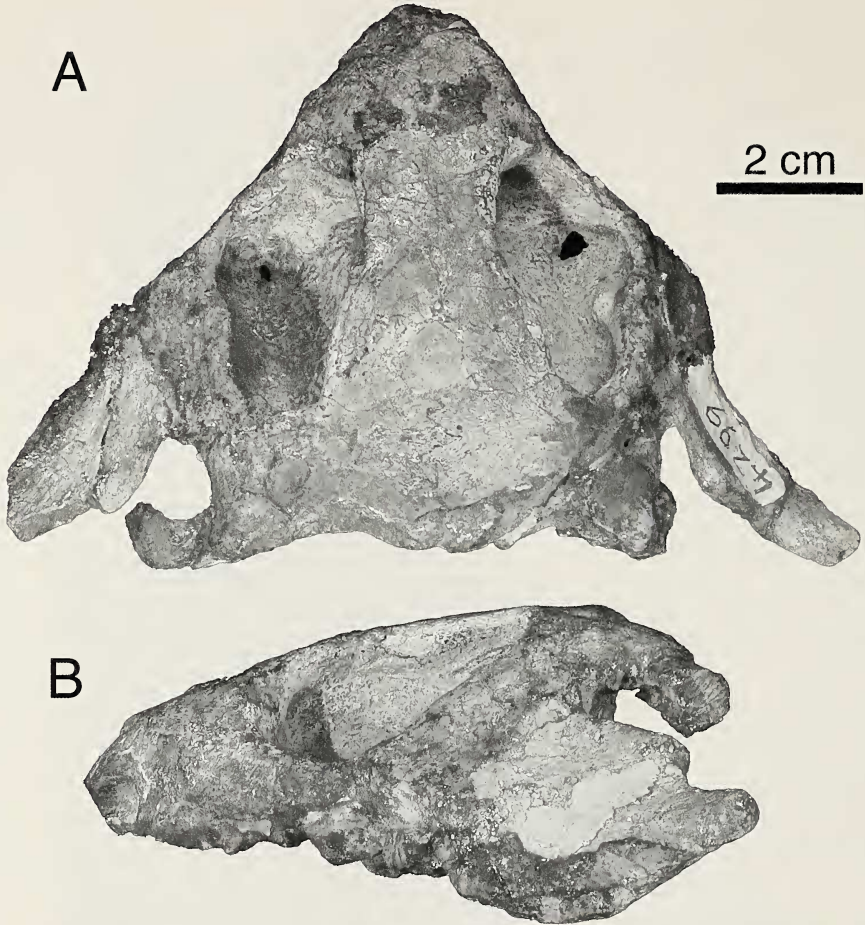


Fig. 5.—*Teratophon spinigenis* (Gow) gen. nov., holotype BP/1/4299, skull. A. Dorsal view. B. Left lateral view.

indicates that *Thelegnathus* has no utility in biostratigraphic considerations of the Beaufort Group. Similarly, the traditional concept of the genus *Thelegnathus* was of a small group of procolophonid species that were endemic to central Gondwana (southern Africa), yet we conclude that there is no compelling evidence for an endemic radiation of procolophonids in the Karoo Basin during the Early to Middle Triassic. Investigations of procolophonid biogeography will be served better by detailed appraisals of the anatomy of all procolophonid taxa and the inclusion of such data into phylogenetic analyses of procolophonid phylogeny. A series of recent studies (Sues and Baird, 1998; Gow, 2000; Spencer, 2000; Sues et al., 2000; Modesto et al., 2001, 2002; Evans, 2001; Reisz and Scott, 2002) suggests that we are undergoing something of a renaissance in procolophonoid research. It is hoped that such work will lead to a better understanding not only of the evolution of these widespread fossil reptiles, but also of the biostratigraphy of the Triassic sediments that preserve them as well.

ACKNOWLEDGMENTS

R. M. H. Smith, S. Kaal, H. Klinger, and K. van Willingham are thanked sincerely for access to facilities, assistance, and hospitality during our visits to the South African Museum. We are also indebted to C. Dube for additional preparation of the “*Thelegnathus*” specimens in the collections of the Bernard Price Institute.

LITERATURE CITED

- BROOM, R. 1905. Preliminary notice of some new fossil reptiles collected by Mr. Alfred Brown at Aliwal North, South Africa. *Records of the Albany Museum*, 1:269–275.
- . 1936. The South African Procolophonia. *Annals of the Transvaal Museum*, 18:387–391.
- CARROLL, R. L., AND W. LINDSAY. 1985. Cranial anatomy of the primitive reptile *Procolophon*. *Canadian Journal of Earth Sciences*, 22:1571–1587.
- DILKES, D. W. 1998. The Early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. *Philosophical Transactions of the Royal Society of London, Series B*, 353:501–541.
- DODICK, J. T., AND S. P. MODESTO. 1995. The cranial anatomy of the captorhinid reptile *Labidosaurikos meachami* from the Lower Permian of Oklahoma. *Palaeontology*, 38:687–711.
- EVANS, S. E. 2001. The Early Triassic ‘lizard’ *Colubrifer campii*: a reassessment. *Palaeontology*, 44:1033–1041.
- GOW, C. E. 1977. New procolophonids from the Triassic *Cynognathus* Zone of South Africa. *Annals of the South African Museum*, 72:109–124.
- . 2000. A new procolophonid (Parareptilia) from the *Lystrosaurus* Assemblage Zone, Beaufort Group, South Africa. *Palaeontologia Africana*, 36:21–23.
- GROENEWALD, G. W., AND J. W. KITCHING. 1995. Biostratigraphy of the *Lystrosaurus* Assemblage Zone. Pp. 35–39, in *Biostratigraphy of the Beaufort Group (Karoo Supergroup)* (B. S. Rubidge, ed.). South African Committee for Stratigraphy, Pretoria.
- HANCOX, P. J., M. A. SHISHKIN, B. S. RUBIDGE, AND J. W. KITCHING. 1995. A three-fold subdivision of the *Cynognathus* Assemblage Zone (Beaufort Group, South Africa) and its palaeogeographic implications. *South African Journal of Science*, 91:143–144.
- IVAKHNENKO, M. F. 1973. Skull structure in the Early Triassic procolophonian *Tichvinskia vjatkensis*. *Paleontological Journal*, 7(4):511–518.
- . 1974. New data on the Early Triassic procolophonids of the USSR. *Paleontological Journal*, 8(3):346–351.
- . 1975. Early Triassic procolophonid genera of Cisuralia. *Paleontological Journal*, 9(1):86–91.
- . 1983. New procolophonids from Eastern Europe. *Paleontological Journal*, 17(2):135–139.
- KITCHING, J. W. 1977. The distribution of the Karoo vertebrate fauna. University of the Witwatersrand, Bernard Price Institute for Palaeontological Research, *Memoir* 1:1–131.
- . 1995. Biostratigraphy of the *Cynognathus* Assemblage Zone. Pp. 40–45, in *Biostratigraphy of the Beaufort Group (Karoo Supergroup)* (B. S. Rubidge, ed.). South African Committee for Stratigraphy, Pretoria.
- LAURENTI, J. N. 1768. *Classis Reptilium. Specimen medicum, exhibens synopsis Reptilium emendatum, cum experimentis circa venena et antidote Reptilium Austriacorum*. J. Thom., Nob. et Trattner, Vienna.
- LAURIN, M., AND R. R. REISZ. 1995. A reevaluation of early amniote phylogeny. *Zoological Journal of the Linnean Society*, 113:165–223.
- LYDEKKER, R. 1890. *Catalogue of the Fossil Reptilia and Amphibia in the British Museum (Natural History)*. Part IV. Containing the Orders Anomodontia, Ecaudata, Caudata, and Labyrinthodontia; and supplement. British Museum (Natural History), London.
- MODESTO, S. P. 1998. New information on the skull of the Early Permian reptile *Captorhinus aguti*. *PaleoBios*, 18:21–35.
- MODESTO, S., H.-D. SUES, AND R. DAMIANI. 2001. A new Triassic procolophonoid reptile and its implications for procolophonoid survivorship during the Permo-Triassic extinction event. *Proceedings of the Royal Society of London, Biological Series*, 268:2047–2052.
- MODESTO, S. P., R. J. DAMIANI, AND H.-D. SUES. 2002. A reappraisal of *Coletta seca*, a basal procolophonoid reptile from the Lower Triassic of South Africa. *Palaeontology*, 45:883–895.
- NEVELING, J., B. S. RUBIDGE, AND P. J. HANCOX. 1999. A lower *Cynognathus* Assemblage Zone fossil from the Katberg Formation (Beaufort Group, South Africa). *South African Journal of Science*, 95:555–556.

- NOVIKOV, I. V. 1991. New data on the procolophonids from the USSR. *Paleontological Journal*, 25(2): 91–105.
- OLSON, E. C. 1947. The family Diadectidae and its bearing on the classification of reptiles. *Fieldiana: Geology*, 11:1–53.
- REISZ, R. R., AND D. SCOTT. 2002. *Owenetta kitchingorum*, sp. nov., a small parareptile (Procolophonia: Owenettidae) from the Lower Triassic of South Africa. *Journal of Vertebrate Paleontology*, 22:244–256.
- SEELEY, H. G. 1888. Researches on the structure, organization and classification of the fossil Reptilia. VI. On the anomodont Reptilia and their allies. *Proceedings of the Royal Society of London*, B44:381–383.
- SPENCER, P. S. 2000. The braincase structure of *Leptopleuron lacertinum* Owen (Parareptilia: Procolophonidae). *Journal of Vertebrate Paleontology*, 20:21–30.
- SUES, H.-D., AND D. BAIRD. 1998. Procolophonidae (Reptilia: Parareptilia) from the Upper Triassic Wolfville Formation of Nova Scotia. *Journal of Vertebrate Paleontology*, 18:525–532.
- SUES, H.-D., P. E. OLSEN, D. M. SCOTT, AND P. S. SPENCER. 2000. Cranial osteology of *Hypsognathus fenneri*, a latest Triassic procolophonid reptile from the Newark Supergroup of eastern North America. *Journal of Vertebrate Paleontology*, 20:275–284.